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RESEARCH ARTICLE

Time perception during apparent biological motion reflects subjective speed of movement, not objective rate of visual stimulation

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Abstract We have investigated links between biological motion perception and time perception. Participants compared the durations of two paired visual frames, inside which task-irrelevant sequences of static body postures were presented. The sequences produced apparent movements of shorter and longer path lengths, depending on the sequential order of body postures (ABC or ACB). Shorter and longer path lengths were paired with shorter and longer interstimulus intervals (ISIs) to produce path/ISI *congruent* sequences with intermediate subjective speeds and path/ISI *incongruent* sequences with slowest and fastest subjective speeds. Participants compared the duration of the visual frames surrounding these sequences; body postures and biological motion were irrelevant. The ability to discriminate the duration of the frames (as measured by the just noticeable difference, JND) was reduced for pairs of path/ISI congruent sequences as compared to pairs of path/ISI incongruent sequences. That is, duration discrimination improved when implied speed differed between the two sequences of a pair compared to when the implied speed was the same. Since stimuli showed no actual movement and were fully matched for lower-level visual input and objective stimulus durations, our findings suggest an involvement of higher-order visual or even motor areas in temporal biases during apparent biological motion perception. We show that apparent speed is the primary dimension of such percepts consistent with a dominant role of movement dynamics in the perception of other people's actions. Our results also confirm an intimate relation between time perception and processing of human movement.

Keywords Biological motion · Apparent motion · Time perception · Visual body perception · Duration discrimination · Action observation · Velocity perception

Introduction

In order to successfully interact in our social environment, humans need to anticipate other people's actions. Accordingly, several authors have argued that the mechanisms of visual perception of human movement serve the primary purpose of predicting other people's actions (Kilner et al. 2007; Wilson and Knoblich 2005). However, in the real world, available visual information is often fragmentary. Predicting actions therefore require brain mechanisms for deriving dynamic representations of movement from actions that are only partially seen (Baker et al. 2001; Graf et al. 2007; Parkinson et al. 2011), or even from purely static displays of the human body (Kourtzi and Shiffrar 1999; Verfaillie and Daems 2002). For example, during apparent biological motion, perception of human movement with natural movement paths (Chatterjee et al. 1996; Orgs and Haggard 2011; Shiffrar and Freyd 1990, 1993) and natural movement dynamics (Grosjean et al. 2007; Orgs et al. 2011) can arise from sequences of purely static body postures.

These studies suggest that biological motion perception involves a cognitive process that constructs a continuous representation of movement, including overall movement

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duration, from minimal static information. Consistent with this suggestion, recent studies explicitly linked human motion perception to subjective time. For example, time perception of static pictures implying human movement is more precise than for displays that do not imply movement (Moscatelli et al. 2011). Other studies using movement videos (Carrozzo and Lacquaniti 2013; Carrozzo et al. 2010; Wang and Jiang 2012), single body postures (Nather et al. 2011) or apparent motion sequences (Orgs et al. 2011; Orgs and Haggard 2011) show that time perception whilst seeing a human movement is biased by the perceived animacy of the static display and by the apparent speed of movement. We suggested one possible cognitive mechanism that could account for these biases, based on a binding process that interpolates the temporal gaps between successive static postures.

However, it remains unclear *how* biological motion should influence time perception. On one view, apparent biological motion mechanisms would replace the static picture sequence with a dynamic percept of movement (Muckli et al. 2005; Yantis and Nakama 1998), by means of feedback from higher-order motion areas to primary visual cortex (Wibral et al. 2009). In the case of apparent *biological* motion such a top-down process would require the involvement of brain areas that are sensitive to sequentially presented body postures, such as the superior temporal sulcus, or even motor cortex (Barraclough et al. 2006; Perrett et al. 2009; Costantini et al. 2005; Stevens et al. 2000). A resulting top-down estimate of *movement* duration may then partially replace bottom-up temporal information purely based on the rate of visual stimulation. We have previously shown that subjective duration of an apparent movement is biased in proportion to the perceived speed of the movement: faster apparent movements are perceived to have shorter durations than slower apparent movements (Orgs et al. 2011). Here, we tested whether the representation of movement duration during apparent biological motion is *primarily* speed-based and would alter the sensitivity of duration discrimination. We created pairs of apparent motion sequences that were identical with respect to implied path and absolute duration. Sequences were therefore fully matched for bottom-up visual and temporal input. However, paired apparent motion sequences could produce either very different or very similar subjective speeds. In congruent sequences, short apparent paths were paired with short ISIs and long apparent paths were paired with long ISIs, producing similar subjective movement speeds. Conversely, in incongruent sequences, short apparent paths were paired with long ISIs and long apparent paths were paired with short ISIs, producing dissimilar subjective movement speeds. Rather than measuring speed-based biases directly *for each* apparent motion sequence (Orgs et al. 2011; Orgs and Haggard 2011), we assessed how biased durations for individual sequences would influence discrimination between the durations of the two sequences in a pair, using a two-alternative forced-choice duration comparison task: if estimates of movement duration were primarily speed-based, differences in objective sequence duration between two sequences with similar apparent movement speeds should be difficult to detect compared to differences in duration between sequences with different apparent speeds. This logic holds even when the sequence pairs were matched for bottom-up visual and temporal information. Such a result would suggest that temporal biases during apparent biological motion are due to an automatic computation of a dynamic representation of movement duration (Freyd 1983) that is based on apparent movement speed, rather than path length or visual rate of stimulation alone (Lappin et al. 1975). Further, since all stimulus sequences are fully matched for lower-level visual and temporal input, it would suggest the involvement of higher-order visual or motor areas that are sensitive to the sequential order of body postures.

Methods

Participants

23 Participants (18 female, 5 male, 20 right-handed, mean age 22 years) were paid £8 or received course credit. All participants gave informed consent prior to the study.

Apparent biological motion sequences

Four whole-body dance movements were choreographed and captured on video. Three greyscale static pictures (initial, intermediate and final posture) were selected from each movement. By swapping the initial and final posture of each of the four movements, eight (ABC or CBA) apparent biological motion sequences (see Fig. 4 in "Appendix") were created. Next, eight additional versions of each of these eight sequences were created by swapping the 2nd and 3rd posture for each short path sequence (e.g. original sequence ABC was transformed to additional sequence ACB). Crucially, these additional versions involved longer movement paths than the original versions. In the original "short path" sequences, the implied paths between 1st and 2nd posture and 2nd and 3rd posture were of identical magnitude (Ratio 1:1). In long path sequences the implied path between 1st and 2nd posture was twice as long as in short path sequences (Ratio 2:1); path length between 2nd and 3rd posture did not change. For all sequences, a feasible movement could always be performed along the shortest path. Shiffrar and Freyd (1993) have shown that when a movement along the shortest path is not restricted by joint or object constraints, participants will always report seeing a feasible movement along the shortest path possible, even for very short ISIs. All apparent movements in our study were therefore feasible, but differed in apparent movement path length. Dance postures were surrounded by a uniformly grey rectangle that subtended approximately 3.1° of visual angle.

Pairs of apparent motion sequences

The three postures comprising a sequence were each displayed for 100 ms and were separated by two ISIs, The ISIs were either congruent with the apparent path length (long path accompanied by long ISI and short path accompanied by short ISI) or incongruent with apparent path length (long path accompanied by short ISI and short path accompanied by long ISI). For path/ISI congruent sequence pairs, the numerical ratio between first and second ISI always reflected the path length ratio between 1st and 2nd, and 2nd and 3rd posture, respectively, that is short movement paths were always combined with two equally short ISIs (short/short, SS), whereas the first ISI in long paths sequences was twice as long as the second ISI (long/short, LS), see Fig. 1. This produced 16 congruent apparent motion sequence pairs, either starting with the short or the long path sequence (ABC/SS–ACB/LS and ACB/LS–ABC/SS). Sixteen path/ISI incongruent sequence pairs were created by combining short paths with long ISIs and long paths with short ISIs (ABC/LS–ACB/SS and ACB/SS–ABC/LS). Importantly, both congruent and incongruent sequence pairs were identical with respect to the sequential order of postures *and* the objective duration difference between long and short path sequences. However, both sequence pairs differed with respect to perceptual similarity of apparent movement speed: in congruent pairs, long and short path sequences are matched for subjective speed, since longer path lengths are combined with proportionally longer ISIs. In contrast, incongruent pairs comprise two sequences with very different apparent speeds, since long paths between 1st and 2nd posture are paired with short ISIs and short paths between 1st and 2nd posture are paired with long ISIs (see Fig. 2).

Task and procedure

Participants compared the duration of first and second sequence for each pair (see Fig. 2). For each trial the first

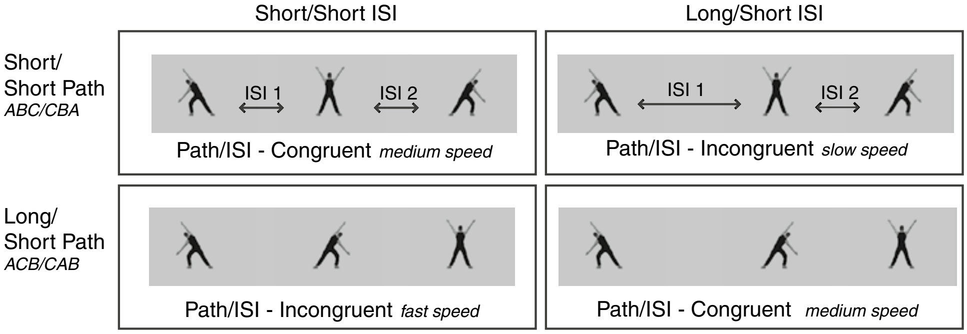

Fig. 1 Experimental design and conditions. Larger and smaller gaps between postures reflect longer and shorter ISIs, respectively. Perceived speed of movement will be fastest for long path/short ISI sequences (*lower left corner*) and slowest for short path/long ISI sequences (*upper right corner*). Congruent sequences should produce intermediate perceived movement speeds. Accordingly, duration discrimination between pairs of incongruent sequences should be easier than duration discrimination between pairs of congruent sequences

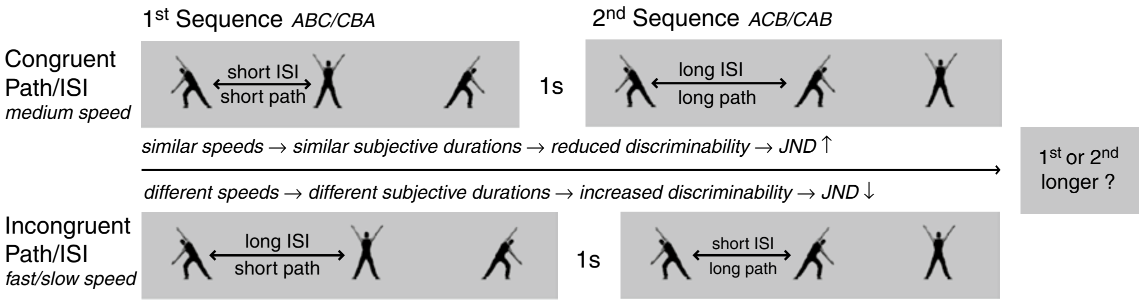

Fig. 2 Example of an experimental trial. Larger and smaller gaps between postures relate to longer and shorter ISIs, respectively. The *grey rectangle* remained visible during the ISIs. Note that congruent and incongruent sequence pairs are fully matched for static visual information and objective duration

sequence served as the standard duration, whereas the second sequence served as the comparison duration (Wearden and Ferrara 1993; Wearden et al. 2007).

We manipulated sequence durations by using eight ISI pairs (SS conditions: 50/50, 100/100, 150/150, 200/200; LS conditions: 100/50, 200/100, 300/150, 400/200). Accordingly, the duration differences between second and first sequence of a pair was 50, 100, 150 and 200 ms if SS sequences were presented first and −50, −100, −150 and −200 ms when LS sequences were presented first.

The experiment comprised five blocks, each containing 64 congruent and 64 incongruent sequence pairs (16 sequence pairs presented at 4 ISI levels and counterbalanced for whether SS or LS sequences occurred first). After a random intertrial interval between 1 and 2 s, participants were presented with pairs of path/ISI congruent or incongruent sequences. Sequences were separated by 1 s. Importantly, participants were instructed to ignore the body postures and to judge *only* the duration of the surrounding grey rectangle visible throughout presentation of the entire picture sequence, including during the ISIs. Participants discriminated the durations of the two grey rectangles surrounding the two sequences, by responding to the question "Which was longer, 1st or 2nd?". Practice trials used two additional sequences not shown in the main experiment.

If apparent movement duration depends primarily on apparent speed, rather than implied path or objective sequence duration alone, identical physical duration differences between first and second sequence should be easier to detect for incongruent pairs, where a speed-based percept of movement duration emphasizes objective duration differences (fast and short vs. slow and long). This contrasts to duration discrimination for congruent pairs, in which the top-down estimate of movement duration would interfere with the bottom-up percept of sequence duration that is purely based on visual rate of stimulation (fast and long vs. slow and short). Accordingly, duration discrimination should be improved for path/ISI incongruent as compared to Path/ISI congruent sequence pairs.

Data analysis

We fitted psychophysical curves to relate the percentages of "longer" responses to actual picture-sequence duration, using logistic regression. The 25, 50 and 75 % values were calculated from each curve. Inspection of these percentiles revealed that they were not normally distributed (Shapiro–Wilks test, $df = 23$, $p < .001$ for both conditions). Accordingly, we calculated the just noticeable difference (JND, 75–25 % percentiles) and the point of subjective equality (PSE, 50 % percentile) for congruent and incongruent sequences in the standard way, but analysed these measures using nonparametric tests only. Median JNDs and PSEs are reported. We also give the interquartile range (IQR) of JNDs and PSEs across subjects as a robust measure of dispersion.

Results

Participants were significantly better at discriminating the objective duration of two rectangles surrounding sequences with incongruent path/ISI combinations as compared to rectangles surrounding path/ISI congruent sequences (Wilcoxon signed-rank test: $W = 2.3$, $p = .023$), with 18 out of 23 participants showing a smaller JND in the incongruent (Median: 256 ms, IQR = 358 ms) as compared to the congruent condition (Median = 326 ms, IQR = 600 ms), see Fig. 3 and supplementary material for individual psychophysical fits.

The PSE for congruent and incongruent sequence pairs was significantly greater than 0 (Friedman test: $\chi^2_F = 14.7$, $df = 2$, $p < .001$), but did not differ between congruent (median = 27 ms, IQR = 51 ms) and incongruent (median: 20 ms, IQR = 33 ms) conditions (Wilcoxon signed-rank test, $W = .06$, $p = .95$). Accordingly, if SS sequences were presented first, the duration of subsequent LS sequences was underestimated (for 17 out of 23 participants). This effect did, however, not depend on path/ISI congruency. Median r^2 goodness of fit for individual subjects was 0.95 (max: 0.76, min: 0.99).

As evident in the single subject data (see supplementary data), seven out of 23 participants exhibited a close to flat psychophysical function in one or both conditions. Excluding those participants, however, produced the same

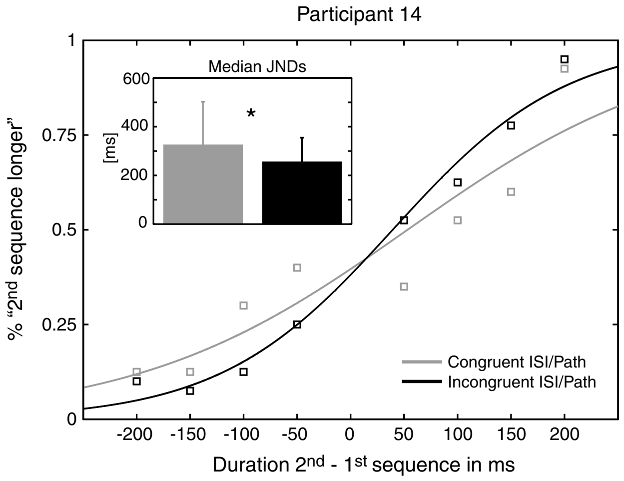

Fig. 3 Percentage of "2nd sequence longer" responses and psychophysical curves (logistic fit) for congruent and incongruent sequences in a representative participant as a function of objective duration difference between two sequences of a pair. Individual psychophysical fits for all 23 participants are available as supplementary material. The embedded *bar graph* shows median JNDs for incongruent (*black*) and congruent (*grey*) sequence pairs (*$p < .05$) for all participants ($N = 23$). *Error bars* depict median absolute deviation

pattern of results: Smaller JNDs in the incongruent as compared to the congruent condition (Wilcoxon signed-rank test: $W = 2.7$, $p = .008$). Since we use the JND as dependent variable, we could not simply exclude outliers based on their discrimination performance (Holmes 2009). Extremely poor performance in the congruent condition, in particular, was found in four subjects. This could in fact result from similar subjective apparent motion speeds, as discussed below.

Discussion

In the present study we show that time perception during apparent biological motion depends on the subjective speed of movement rather than objective duration or implied path alone. Our findings are consistent with the idea that velocity is a directly perceived attribute of motion. The brain does not appear to compute movement velocity by combining available information about spatial and temporal extent but rather forms an estimate of movement velocity that is based on relative change in both dimensions (Lappin et al. 1975). It is this subjective velocity that, in turn, dominates time perception.

This effect is most pronounced for small duration differences around 50 ms. Biases in time perception are typically observed in this temporal range. Examples include such diverse manipulations as stimulus size (Ono and Kitazawa 2009), action preparation (Hagura et al. 2012) or TMS (Bueti et al. 2008). Importantly, speed-based temporal biases occur automatically and do not require explicit attempts to "see" movement. Since congruent and incongruent sequences were identical with respect to their basic visual and temporal features (sequence of static postures and ISIs), our findings cannot be explained by differences in bottom-up visual or temporal processing or general attention. Biases in subjective duration have previously been related to the amount of neural energy spent on a given task (Eagleman 2008). Our results imply that subjective durations in congruent sequences are more similar to each other than in incongruent sequences. Accordingly, shorter sequences become subjectively longer and longer sequences become subjectively shorter in congruent than in incongruent sequences. Such a finding requires a directional influence of perceived movement speed on subjective duration that does not easily map onto theoretical accounts based on neural energy. Our results suggest that time perception must be related to the perceived dynamics of the visual stimulus and not purely to magnitude and processing factors such as neural energy.

Previous work from our group (Orgs et al. 2011) as well as others (Shiffrar and Freyd 1990, 1993) has shown that (apparent) biological motion is qualitatively different from apparent motion of simple visual shapes and induces temporal distortions that are specifically induced by the shape of the human body (Moscatelli et al. 2011; Carrozzo et al. 2010; Carrozzo and Lacquaniti 2013; Wang and Jiang 2012).

Accordingly, we propose that apparent biological motion automatically generates a specific percept of movement speed. Because of the robust relation between speed and duration in both actual human movement (Tanaka et al. 2006), and biological motion perception (Orgs et al. 2011; Grosjean et al. 2007), these apparent modulations of speed lead to differently perceived movement durations. Specifically, our results show that such a speed-based, top-down representation of movement duration contributes to duration processing in otherwise identical apparent motion sequence pairs. We can only speculate on the mechanism of this top-down influence, given that our experiment is purely behavioural. However, our results are consistent with previous reports of involvement of higher-order visual or even motor areas in apparent biological motion perception (Barraclough et al. 2006; Perrett et al. 2009; Costantini et al. 2005; Stevens et al. 2000). This tendency for movement speed to bias movement durations may be important in predicting the progress of others' actions.

Moscatelli et al. (2011) reported improved time perception for implied motion photographs. Similarly, studies using partially occluded point-light walkers suggest very accurate simulation of objective durations in displays of biological motion (Graf et al. 2007; Parkinson et al. 2011). However, in our study time perception only improves if kinematic features of the observed movement (speed) emphasize physical stimulus duration (fast and short/slow and long), but deteriorates if apparent movement kinematics disguise objective duration differences (fast and long/slow and short). Thus, in contrast to previous studies using either biological motion videos or implied motion photographs, we can distinguish between a top-down nonlinear estimate of movement duration and a bottom-up estimate of stimulus duration based on rate of visual stimulation. Our findings show that for small duration differences, temporal judgements are primarily based on speed-based movement duration rather than rate of visual stimulation.

Apart from changes in sensitivity to duration differences, our data show that longer second sequences (with a long/short ISI pair) were subjectively shortened if the first sequence was objectively shorter (short/short ISI pair). This finding resembles the "time-shrinking" illusion in rhythm perception (Ten Hoopen et al. 1995, 2006): The subjective duration of a longer interval following a shorter interval is reduced to produce perception of a more regular temporal pattern. In other words, sequentially presented intervals with similar, relatively short durations tend to "assimilate" longer durations. In addition to overall poor performance in some participants, such assimilation effects may have limited average performance levels to 75 % correct by subjectively reducing the duration of the “long” interval in long/short ISI pairs. Importantly, however, such temporal distortions induced by multiple time intervals did not differ between congruent and incongruent sequence pairs and can therefore not explain our findings.

Similarly, a recent study suggests that using a temporal reproduction task, stimuli with a constant velocity profile appear to have subjectively longer durations than stimuli with a variable velocity profile that approximates human movement kinematics (Gavazzo et al. 2013). However, in our study incongruent sequence pairs with varying velocities were not perceived to have overall shorter durations than congruent sequences with consistent velocities. This suggests that discriminability between sequences was mainly influenced by overall sequence speed rather than changes in acceleration. Future studies may address the relative contribution of velocity and acceleration on subjective time in greater detail.

To summarize, our experiment provides evidence for three claims about human biological motion perception. First, consistent with previous findings (Orgs et al. 2011; Orgs and Haggard 2011), the perception of human movement involves a top-down process that operates automatically and produces dynamic movement from purely static input. Second, this process influences other aspects of cognition such as time perception. Third, and most specifically, biological motion perception involves a computation of movement duration that combines displacement and time information to construct a mental composite that primarily reflects apparent speed of movement. This speed-based estimate of movement duration seems to be the basic perceptual dimension of apparent biological motion since it partially replaces available information about objective stimulus duration. Accordingly, time perception during biological motion may improve or deteriorate, depending on whether this top-down, speed-based estimate of movement duration emphasizes (fast and short/slow and long) or contradicts (fast and long/slow and short) the bottom-up estimate of stimulus duration.

Our findings are based on laboratory experiments with carefully selected static stimuli presented at ISIs that produce apparent biological motion. However, the automatic mechanism that we reveal, whereby speed-based apparent biological motion can influence time perception, may be useful in everyday life also. Visual input about other people’s actions in the real world is often incomplete, and the brain may often rely on such internal dynamic representations, rather than on available visual bottom-up information alone (Freyd 1983). Anticipating actions on the basis of movement speed is more efficient, since it requires visual information sampling over a shorter period of time than an indirect computation based on time and space alone (Lappin et al. 1975; Gibson 1966). Our experience of time itself is intimately connected to perceiving the actions of other people.

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Conflict of interest The authors declare that they have no conflict of interest.

Appendix

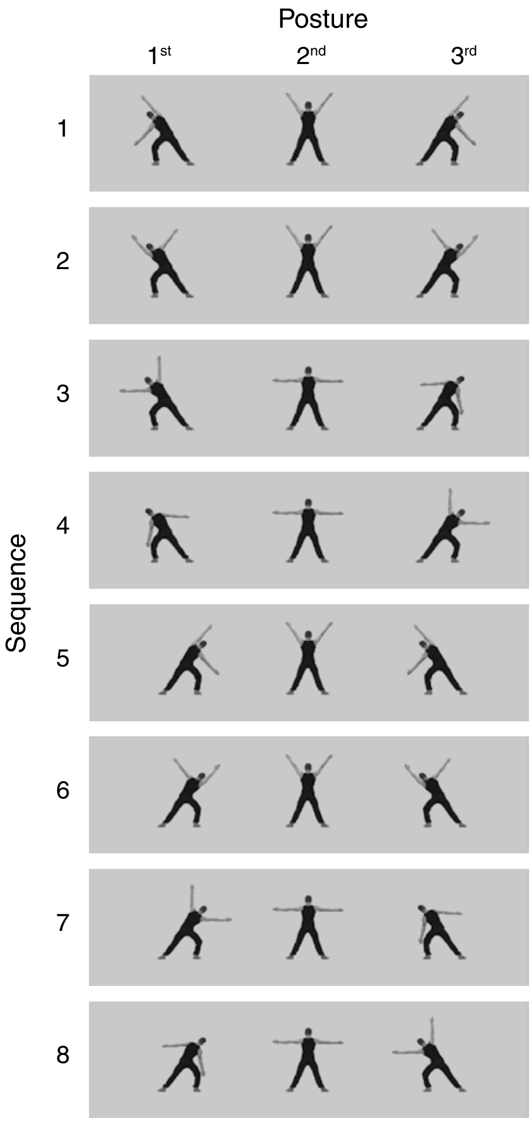

Fig. 4 All eight apparent movement sequences used in the main experiment. Sequences 5–8 are reversals of sequences 1–4

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